POME ANATOMY OF ROSACEAE SUBFAM. MALOIDEAE, WITH SPECIAL REFERENCE TO *PYRUS*[1]

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Abstract

Two anatomical features of the pome in Rosaceae subfam. Maloideae are investigated: sclereid type and epidermal structure. The large and irregular groups of sclereids in *Pyrus* are different from those in *Sorbus* subgenera *Aria*, *Chamaemespilus*, and *Cormus*, and similar to those in *Cydonia*. In addition, multilayered epidermis, hitherto unreported from *Pyrus*, is documented in *Pyrus* sect. *Pashia*. Consequently, both the monophyly of *Pyrus* and its current sectional classification are supported.

The taxonomy of Rosaceae subfam. Maloideae is problematic in terms of generic delimitation. The inconsistency of the main generic characters has generated a great deal of disagreement in the taxonomic treatment of the group. A representative of the more synthetic view was de Candolle (1825), who included in *Pyrus* species now usually referred to *Malus*, *Photinia*, *Eriolobus*, and *Sorbus*. This classification was followed by Sax (1931) and Robertson (1974). Conversely, Decaisne (1874) and Koehne (1890) used smaller generic concepts. They treated *Pyrus* in a more restricted sense, and split off *Photinia*, *Malus*, and *Sorbus*. A comprehensive review of taxonomic treatments applied to these genera was provided by Robertson et al. (1991).

Malus, *Cydonia*, *Sorbus* subg. *Aria* Pers., and *Sorbus* subg. *Chamaemespilus* (Medik.) K. Koch have all been advanced as close relatives of *Pyrus* (Weber, 1964; Iketani & Ohashi, 1991; Campbell et al., 1995). According to Decaisne (1874), pomes of both *Sorbus* subg. *Aria* and *S.* subg. *Chamaemespilus* are characterized by their heterogeneous flesh. Flesh heterogeneity of pomes in subfamily Maloideae was studied by Kovanda (1961) and Iketani and Ohashi (1991), who showed that it was caused by groups of parenchyma cells filled with tannic substances. *Cydonia*, formerly included in *Pyrus* by Linnaeus (1753), and closely related to it according to Robertson et al. (1991), is easily distinguishable by its solitary flowers and numerous ovules per locule. *Malus* is separated by its connate styles (free in *Pyrus*). This feature is consistent, but may be difficult to evaluate in practice. Thus, Bailey (1949) reported the structure of the flower cluster as the most obvious distinction between *Pyrus* and *Malus*: the *Pyrus* inflorescence has a rachis from which the pedicels emerge, while that of *Malus* has an umbellate structure. Nevertheless, Robertson et al. (1991) showed that both *Pyrus* and *Malus* could have corymbs, panicles, or umbels. Finally, the supposed scarcity or absence of sclereids in the pomes of *Malus* was contested by several authors, including Rehder (1940), Browicz (1969), Terpó (1968), and Iketani and Ohashi (1991). Robertson et al. (1991) reported that *Malus* may have abundant sclereids under the skin and around the core of the pomes. Hybridization and grafting experiments provide additional data about *Pyrus* relationships. According to Taylor (1983) *Pyrus* and *Malus* do not hybridize and cannot be grafted one to the other. They also differ in flavonoid composition (Williams, 1982). However, Weber (1964) and Robertson (1974) reported that *Pyrus*, *Malus*, and *Cydonia* can and do hybridize among themselves.

According to Rohrer et al. (1991: 78), the skin of the pomes of subfamily Maloideae "consists of a single epidermal layer of tightly packed, anticlinally flattened, rectangular cells covered with a cuticle." Such an epidermal structure has been described for *Crataegus* (Akhunova, 1986), *Malus* (Clements, 1935), and *Amelanchier* (Olson &

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Steeves, 1982). On the other hand, Miller (1984) reported a multilayered epidermis in *Mespilus germanica* L. Our survey of anatomical characteristics of pomes of subfamily Maloideae has documented the occurrence of a multilayered epidermis in both *Pyrus* and *Sorbus torminalis* (Aldasoro et al., 1998).

The supraspecific taxonomy of *Pyrus* is also controversial. Decaisne (1871–1872) recognized 23 species arranged in six informal groups. Koehne (1890) described two sections: *Pashia* and *Achras*. Fedorov (1954) recognized four sections: *Pashia*, *Pyrus* (= sect. *Achras* Koehne), *Xeropyrenia* Fed., and *Argyromalon* Fed. Tuz (1972) reduced these to two, *Pashia* and *Pyrus*, each with several subsections. Terpó (1985) added his section *Pontica*, but the classification of Tuz (1972) was accepted by Browicz (1993), who pointed out that the two sections could be distinguished by certain obscure characters. According to Browicz (1993) the more operative ones are: the sepal persistence on the pome, the presence or absence of whitish lenticels, and the thickness and flexibility of the pedicels in fruit. The character states of section *Pyrus* are: sepals persistent, white lenticels absent, and thick, stiff pedicels; and of section *Pashia:* sepals deciduous, white lenticels present, and thin, flexible pedicels. Nevertheless, these characters showed some inconsistency; for example, several species of section *Pashia* may have thick pedicels.

The aim of the present work is to investigate some anatomical features of subfamily Maloideae pomes with special reference to *Pyrus*, and to discuss their bearing on the taxonomic issues detailed above. The currently accepted concept of *Pyrus* is that of Decaisne (1874), and the sectional division of the genus that proposed by Tuz (1972), because they are better supported by morphological and anatomical data (Robertson et al., 1991; Browicz, 1993; Aldasoro et al., 1996).

Material and Methods

Pomes were collected (see Table 1) and preserved in Kew mixture (Forman & Bridson, 1989). They were cut with a razor blade both longitudinally and transversely in order to examine the internal structure. Thin hand-cuts were taken in the proximal third of the pome and photographed by light microscopy. Other cuts were made with a SLEE-MAINZ-MTC microtome and stained with Fasga mixture (Tolivia & Tolivia, 1987). In some cuts, malachite green was used to stain the sclereids. For scanning microscopy, dried pomes were cut, glued to aluminum stubs, coated with 40–50 nm gold and examined in a JEOL-TSM T330A scanning electron microscope at 20 kV.

Results

Usually, sclereids are present in the flesh of pomes of subfamily Maloideae. They may occur under the skin, in the core or spread throughout the flesh, isolated or in groups, and vary considerably in shape and size.

Four main sclereid types could be distinguished in the flesh (Table 1): isolated sclereids, as in *Rhaphiolepis*; small groups (less than 10), as in *Amelanchier, Chaenomeles, Cotoneaster, Crataegus, Eriobotrya, Malus, Photinia*, and *Sorbus* subgenera *Sorbus* and *Torminaria*; large but irregular groups, as in *Pyrus* (Fig. 1A, B) and *Cydonia*; and large and rounded groups, as in *Sorbus* subgenera *Aria, Chamaemespilus*, and *Cormus* (Fig. 1C, D).

The groups of sclereids in *Pyrus* and *Cydonia* are remarkably dense (over 50 sclereids can be counted in an equatorial section) and have an irregular outline, while in *Sorbus* subgenera *Aria, Chamaemespilus*, and *Cormus* they comprise less than 40 sclereids and have an elliptic outline (Fig. 1C, D). Some consistent differences in the size and shape of these sclereids were observed (Table 1). *Pyrus* and *Cydonia* sclereids are smaller and have a smaller lumen (40–80 μm long; lumen diameter 10–51 μm; wall thickness 10–20 μm) than those of *Sorbus* subgenera *Aria, Chamaemespilus*, and *Cormus* (110–240 μm long; lumen diameter 76–180 μm; wall thickness 6–32 μm) (Fig. 1). Sclereids in pomes of *Malus* were isolated or in small groups, and were larger and with a greater lumen diameter (75–360 μm long; lumen diameter 12–310 μm; wall thickness 15–80 μm) than those of *Pyrus* pomes.

We were able to study the pomes of 16 of the 38 species of *Pyrus* accepted by Browicz (1993): 9 belonging to section *Pyrus*, and 7 to section *Pashia* (Table 1). A multilayered epidermis was found only in *Pyrus* sect. *Pashia*, while species of section *Pyrus* had only a single layer of epidermal cells that produced a thick cuticle (Fig. 2C, D). The remaining species of subfamily Maloideae showed a single-layered epidermis, except for *Mespilus germanica* and *Sorbus torminalis* (Table 1; Miller, 1984; Aldasoro et al., 1998).

In *Pyrus*, the multilayered epidermis has 3–6 layers of cells, each layer with a cuticular membrane. These cells are tangentially compressed and filled with tannic substances (Fig. 2A, B). They develop from a tangential meristem layer that is somewhat similar to the phellogen, a meristem that ap-

Table 1. Pome epidermal type and sclereid features in Rosaceae subfam. Maloideae. The data are means of five samples from the specimens cited.

Taxon	Flesh sclereid groups	Sclereid length (μm)	Sclereid lumen diameter (μm)	Sclereid wall thickness (μm)	Pome epidermis (ML: multilayered, SL: single-layered)	Source of data	Material studied
Amelanchier canadensis (L.) Medik.	small groups	67	35	12	SL	this study	cult. MA, *Aldasoro 561* (MA)
Chaenomeles japonica (Thunb.) Lindl.	small groups	55	35	10	SL	this study	cult. MA, *Aldasoro 544* (MA)
Cotoneaster buxifolius Wall. ex Lindl.	small groups	63	40	11	SL	this study	cult. MA, *Aedo 3891* (MA)
C. integerrimus Medik.	small groups	40	10	7	SL	this study	cult. MA, *Aldasoro 580* (MA)
Crataegus azarolus L.	small groups	98	90	10	SL	this study	Spain, *Soler 779* (MA)
C. ×*ruscinonensis* Gren. & Blanc	small groups	100	70	15	SL	this study	Spain, *Soler 777* (MA)
Cydonia oblonga Mill.	large and irregular groups	50	25	10	SL	this study	Spain, *Aldasoro 561* (MA)
Eriobotrya bengalensis (Roxb.) Hook.	small groups	80	40	22	SL	this study	cult. MA, *Aldasoro 717* (MA)
E. japonica (Thunb.) Lindl.	small groups	100	20	24	SL	this study	cult. MA, *Aldasoro 715* (MA)
E. petiolata Hook.	small groups	120	70	25	SL	this study	cult. MA, *Aldasoro 714* (MA)
E. tengyuehensis W. W. Sm.	small groups	110	12	45	SL	this study	cult. MA, *Aldasoro 716* (MA)
Hesperomeles ferruginea Lindl.	absent	—	—	—	SL	this study	Colombia, *Cuatrecasas 28890* (MA)
H. lanuginosa Hook.	absent	—	—	—	SL	this study	Peru, *Cano 4179* (MA)
H. salicifolia (C. Presl) Abrams	absent	—	—	—	SL	this study	California: USA, *Bartholomew 1479* (MA)
Malus baccata (L.) Borkh.	small groups	127	82	20	SL	this study	cult. K, *Aldasoro 691* (MA)
M. florentina (Zucc.) C. K. Schneid.	small groups	90	40	24	SL	this study	cult. K, *Aldasoro 634* (MA)
M. fusca (Raf.) C. K. Schneid.	small groups	80	55	20	SL	this study	cult. MA, *Aldasoro 539* (MA)
M. halliana Koehne	small groups	75	30	20	SL	this study	cult. Hillier Gardens, *Aldasoro 606* (MA)
M. ioensis (Wood) Britton	small groups	153	120	20	SL	this study	cult. K, *Aldasoro 719* (MA)
M. kansuensis (Batalin) C. K. Schneid.	small groups	100	12	80	SL	this study	cult. K, *Aldasoro 681* (MA)
M. sieboldii Rehder	small groups	78	35	20	SL	this study	cult. K, *Aldasoro 648* (MA)
M. sikkimensis Koehne ex C. K. Schneid.	small groups	127	95	15	SL	this study	cult. K, *Aldasoro 689* (MA)
M. trilobata (Labill.) C. K. Schneid.	small groups	360	310	25	SL	this study	cult. K, *Aldasoro 665* (MA)
M. tschonoskii (Maxim.) C. K. Schneid.	small groups	150	120	18	SL	this study	cult. K, *Aldasoro 643* (MA)
M. yunnanensis (Franch.) C. K. Schneid.	small groups	180	100	40	SL	this study	cult. Hillier Gardens, *Aldasoro 635* (MA)

Table 1. Continued.

Taxon	Flesh sclereid groups	Sclereid length (µm)	Sclereid lumen diameter (µm)	Sclereid wall thickness (µm)	Pome epidermis (ML: multilayered, SL: single-layered)	Source of data	Material studied
Mespilus germanica L.	absent	—	—	—	ML	Miller (1984), and this study	Spain, *Navarro 1166* (MA)
Photinia beauverdiana C. K. Schneid.	small groups	100	35	25	SL	this study	cult. K, *Aldasoro 658* (MA)
Ph. davidiana (Decne.) Cardot	small groups	64	40	12	SL	this study	cult. MA, *Aldasoro 709* (MA)
Ph. melanocarpa (Michx.) K. R. Robertson & J. B. Phipps	small groups	100	25	12	SL	this study	cult. MA, *Aldasoro 710* (MA)
Ph. pyrifolia (Lam.) K. R. Robertson & J. B. Phipps	small groups	70	40	14	SL	this study	cult. Hillier Gardens, *Aldasoro 594* (MA)
Ph. serratifolia (Desf.) Kalkman	small groups	45	10	18	SL	this study	cult. MA, *Aldasoro 708* (MA)
Pyrus sect. *Pyrus*							
P. armeniacus Mulk.	large and irregular groups	64	34	16	SL	this study	Armenia, unknown collector (MA-474349)
P. bourgeana Decne.	large and irregular groups	60	10	15	SL	this study	cult. MA, *Aldasoro 131* (MA)
P. communis L.	large and irregular groups	—	—	—	SL	this study	Spain, *Monasterio et al. 1168* (MA)
P. elaeagnifolia Pall.	large and irregular groups	42	25	10	SL	this study	cult. K, *Aldasoro 690* (MA); Macedonia: [Yugoslavia] *Frost-Olsen 2634* (MA)
P. georgica Kuth.	large and irregular groups	56	24	16	SL	this study	Georgia, unknown collectors (MA-417326, MA-417326)
P. nivalis Jacq.	large and irregular groups	78	40	20	SL	this study	cult. Hillier Gardens, *Aldasoro 641* (MA)
P. salicifolia Pall.	large and irregular groups	50	10	15	SL	this study	cult. MA, *Aldasoro 690* (MA); Armenia, unknown collector (MA-298629)
P. spinosa Forssk.	large and irregular groups	58	20	20	SL	this study	Spain, *Navarro et al. 1405* (MA)
P. syriaca Boiss.	large and irregular groups	70	31	19	SL	this study	cult. K, *Aldasoro 668* (MA)
Pyrus sect. *Pashia*							
P. betulifolia Bunge	large and irregular groups	58	30	20	ML	this study	cult. K, *Aldasoro 670* (MA)
P. calleryana Decne.	large and irregular groups	—	—	—	ML	this study	cult. K, *Aldasoro 707* (MA)

Table 1. Continued.

Taxon	Flesh sclereid groups	Sclereid length (µm)	Sclereid lumen diameter (µm)	Sclereid wall thickness (µm)	Pome epidermis (ML: multilayered, SL: single-layered)	Source of data	Material studied
P. cordata Desv.	large and irregular groups	50	10	20	ML	this study	Spain, *Aedo 2477* (MA)
P. pashia Buch.-Ham.	large and irregular groups	76	51	10	ML	this study	cult. Hillier Gardens, *Aldasoro 641* (MA); cult. K, *Aldasoro 683* (MA)
P. phaeocarpa Rehder	large and irregular groups	—	—	—	ML	this study	cult. K, *Aldasoro 669* (MA)
P. pyrifolia (Burm. f.) Nakai	large and irregular groups	60	25	17	ML	this study	cult. K, *Aldasoro 667* (MA)
P. ussuriensis Maxim.	large and irregular groups	60	28	17	ML	this study	cult. K, *Aldasoro 676* (MA)
Rhaphiolepis ×*delacourii* André	isolated	90	60	15	SL	this study	cult. K, *Aldasoro 666* (MA)
R. umbellata (Thunb.) Makino	isolated	60	20	10	SL	this study	cult. MA, *Aldasoro 545* (MA)
Sorbus subg. *Sorbus*							
Sorbus aucuparia L.	small groups	55	30	10	SL	Aldasoro et al. (1998)	Spain, *Aedo 3383* (MA)
S. conmixta Hedl.	small groups	60	35	12	SL	this study	cult. MA, *Aldasoro 553* (MA)
S. esserteauiana Koehne	small groups	120	35	12	SL	this study	cult. MA, *Aldasoro 541* (MA)
S. forrestii McAlister & Gillham.	small groups	122	100	10	SL	this study	cult. K, *Aldasoro 602* (MA)
S. hupehensis C. K. Schneid.	small groups	70	40	13	SL	this study	cult. MA, *Aldasoro 550* (MA)
S. hybrida L.	small groups	60	30	10	SL	Aldasoro et al. (1998)	Spain, *Aldasoro 453* (MA)
S. vilmorinii C. K. Schneid.	small groups	124	100	13	SL	this study	cult. NSS, *Aldasoro 629* (MA)
Sorbus subg. *Aria*							
Sorbus alnifolia (Siebold & Zucc.) K. Koch	large and rounded groups	150	110	21	SL	this study	cult. K, *Aldasoro 672* (MA)
S. aria (L.) Crantz	large and rounded groups	140	100	14	SL	Aldasoro et al. (1998)	Spain, *Aedo 3380* (MA)
S. folgneri (C. K. Schneid.) Rehder	large and rounded groups	127	76	25	SL	this study	cult. MA, *Aldasoro 711* (MA)
S. hajastana Gabrielian	large and rounded groups	165	135	15	SL	this study	cult. K, *Aldasoro 679* (MA)
S. hedlundii C. K. Schneid.	large and rounded groups	134	95	20	SL	this study	cult. Hillier Gardens, *Aldasoro 639* (MA)

Table 1. Continued.

Taxon	Flesh sclereid groups	Sclereid length (µm)	Sclereid lumen diameter (µm)	Sclereid wall thickness (µm)	Pome epidermis (ML: multilayered, SL: single-layered)	Source of data	Material studied
S. hemsleyi (C. K. Schneid.) Rehder	large and rounded groups	120	100	25	SL	this study	cult. K, *Aldasoro 651* (MA)
S. japonica (Decne.) Hedl.	large and rounded groups	140	90	20	SL	this study	cult. K, *Aldasoro 704* (MA)
S. keissleri (C. K. Schneid.) Rehder	large and rounded groups	240	180	21	SL	this study	cult. K, *Aldasoro 652* (MA)
S. lanata (D. Don) Schauer	large and rounded groups	130	100	15	SL	this study	cult. NSS, *Aldasoro 624* (MA)
S. pallescens Rehder	large and rounded groups	140	100	21	SL	this study	cult. K, *Aldasoro 700* (MA)
S. subfusca (Ledeb.) Boiss.	large and rounded groups	140	120	20	SL	this study	cult. K, *Aldasoro 687* (MA)
S. takhtajanii Gabrielian	large and rounded groups	178	112	32	SL	this study	cult. K, *Aldasoro 680* (MA)
S. vestita (Wall. ex G. Don) Lodd.	large and rounded groups	205	160	27	SL	this study	cult. K, *Aldasoro 658* (MA)
S. yuana Spongberg	large and rounded groups	110	98	18	SL	this study	cult. Wakehurst Garden, *Aldasoro 703* (MA)
S. zahlbruckneri C. K. Schneid.	large and rounded groups	123	90	20	SL	this study	cult. K, *Aldasoro 702* (MA)
Sorbus subg. *Chamaemespilus*							
S. chamaemespilus (L.) Crantz	large and rounded groups	140	120	30	SL	Aldasoro et al. (1998)	Spain, *Aedo 3140* (MA)
Sorbus subg. *Cormus*							
Sorbus domestica L.	large and rounded groups	130	120	6	SL	Aldasoro et al. (1998)	Spain, *Aldasoro 560* (MA)
Sorbus subg. *Torminaria*							
Sorbus torminalis (L.) Crantz	small groups	70	60	20	ML	Aldasoro et al. (1998)	Spain, *Navarro 1380* (MA)

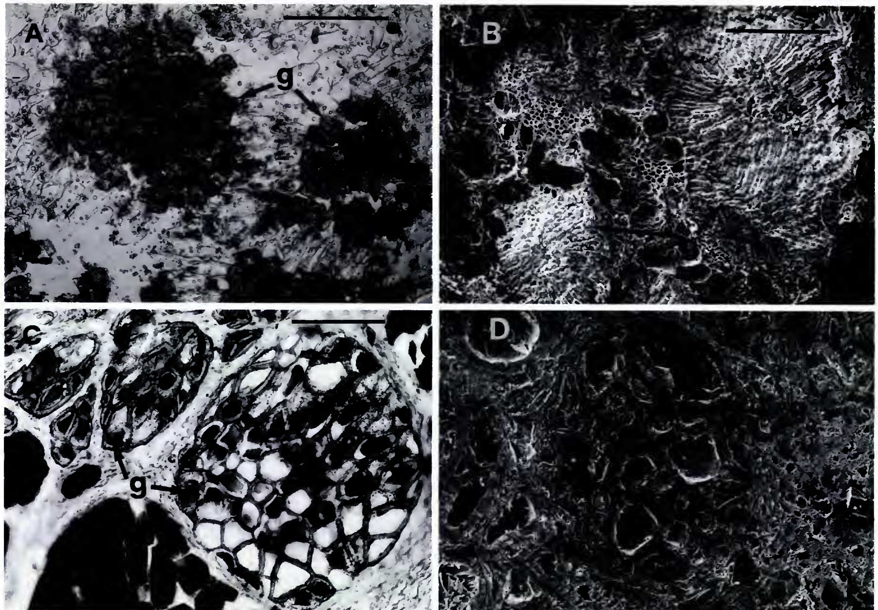

Figure 1. SEM and optical photomicrographs of the groups of sclereids (g) in *Pyrus* and *Sorbus* pomes. —A. Optical photomicrograph of *Pyrus syriaca* (*Aldasoro 668*) showing large irregular groups of sclereids. —B. SEM photomicrograph of *P. spinosa* (*Navarro et al. 1405*) showing large irregular groups of sclereids. —C. Optical photomicrograph of *Sorbus lanata* (*Aldasoro 624*) showing large rounded groups of sclereids. —D. SEM photomicrograph of *S. pallescens* (*Aldasoro 700*) showing large rounded groups of sclereids. Scale bars: A = 500 μm; B: 500 μm; C: 200 μm; D: 100 μm.

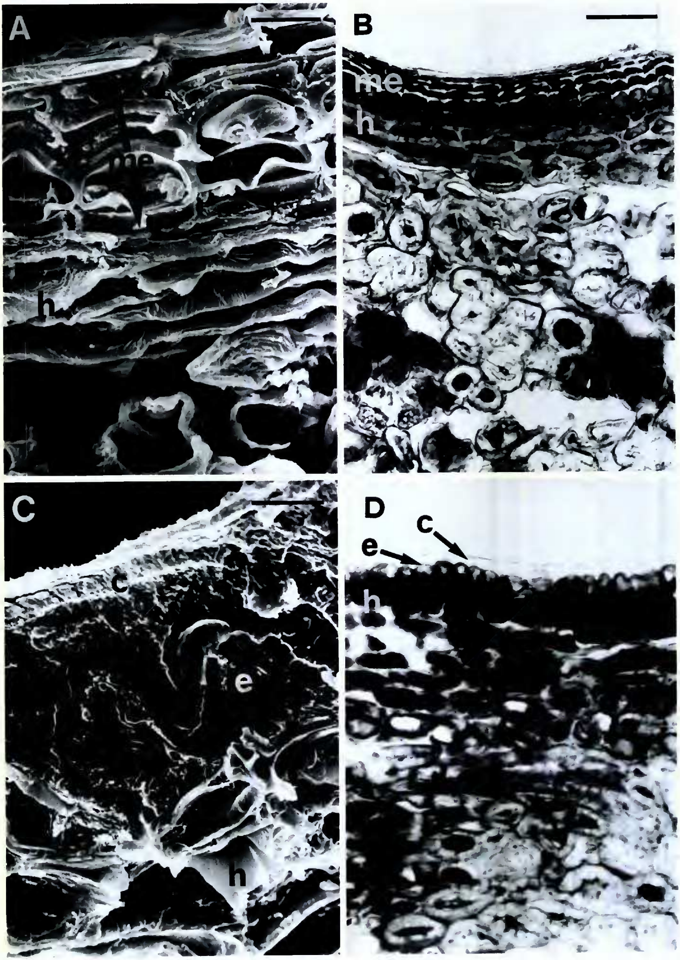

Figure 2. SEM and optical photomicrographs of the epidermis in *Pyrus* pomes. —A. SEM photomicrograph of *Pyrus pashia* (*Aldasoro 641*) showing the multilayered epidermis (me) and the hypodermis (h). —B. Optical photomicrograph of *P. pashia* (*Aldasoro 641*) showing the multilayered epidermis (me) and the hypodermis (h). —C. SEM photomicrograph of *P. spinosa* (*Navarro et al. 1405*) showing the one-layered epidermis (e), the cuticle (c) and the hypodermis (h). —D. Optical photomicrograph of *P. spinosa* (*Navarro et al. 1405*) showing the one-layered epidermis (e), the cuticle (c) and the hypodermis (h). Scale bars: A = 10 μm; B: 25 μm; C: 5 μm; D: 20 μm.

pears in the subepidermal region of the incipient lenticel. Like the phellogen, the tangential meristem of the multilayered epidermis divides periclinally, producing layers of cells that undergo a progressive exfoliation. In some cases, it was observed that lenticel concrescence occurred prior to the development of a multilayered cuticle.

Discussion

The hypothesis that *Pyrus* and *Cydonia* are sister taxa was advanced by Rohrer et al. (1994) on the basis of a single presumed synapomorphy: a pit in the floral cup surrounding the style group. The data contributed by Campbell et al. (1995) on ITS DNA sequences also support this view. Our studies show that these genera have sclereids similar in size, structure, and arrangement, which strengthens this idea. However, several other characters uphold the continued recognition of *Cydonia* and *Pyrus* as separate genera: *Cydonia* has pluriovulate carpels, leaves with no adaxial glands, and solitary, pink flowers. In contrast, *Pyrus* has biovulate carpels, adaxial leaf glands, and corymbose, white flowers. Iketani and Ohashi (1991), Sterling (1966a, b), and Kalkman (1988) proposed that *Pyrus* may have branched from the ancestor of *Cydonia* before the latter acquired the pluriovulate condition. Thus, the previously mentioned characters would support the monophyly of *Pyrus* sensu Decaisne (1874). This would be of remarkable interest in subfamily Maloideae, the genera of which have rather few apomorphic character states. However, our data do not support a close relationship between *Pyrus* and *Malus*, since they have different types of sclereid groups.

The distribution of the multilayered pome epidermis in *Pyrus* seems to support the infrageneric classification proposed by Tuz (1972) and Browicz (1993), at least in terms of the sectional division. This is interesting because, as mentioned previously, some of Browicz's sectional characters, such as pedicel thickness, are variable: the pedicels of *P. pyrifolia* and *P. pashia* (sect. *Pashia*) are thicker than those of some species in section *Pyrus*.

Some other taxa of subfamily Maloideae (*Mespilus*, *Sorbus*) may also have a multilayered pome epidermis. According to Phipps et al. (1991) and Campbell et al. (1995), *Mespilus*, *Pyrus*, and *Sorbus* (subg. *Torminaria*) are not closely related. Moreover, pomes with a multilayered epidermis were not present in any of the primitive genera of Maloideae studied (i.e., *Cotoneaster*, *Eriobotrya*, *Heteromeles*, *Photinia*, and *Rhaphiolepis*; primitive according to Phipps et al., 1991; Campbell et al., 1995). Consequently, a multilayered epidermis is most parsimoniously viewed as derived, and it seems an independently acquired character state in these genera. The adaptative role of the multilayered epidermis is unknown, but it may be related to seed dispersal by mammals. All pomes of subfamily Maloideae studied with a multilayered epidermis present traits associated with mammalian zoochory syndromes: green or brown skin inconspicuous to birds, copious lenticels permitting scent to emanate, seeds protected against mammal-stomach gastric juices by many sclereids, tannins inhibiting bacterial or fungal damage in the ground, and high fiber content (Herrera, 1989).

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